INTERACTIONS OF PREDACEOUS KATYDIDS (ORTHOPTERA: TETTIGONIIDAE) WITH NEOTROPICAL SOCIAL WASPS (HYMENOPTERA: VESPIDAE): ARE WASPS A DEFENSE MECHANISM OR PREY?¹

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ABSTRACT: Field observations of interactions between predaceous tettigoniids, *Phlugis poecila* and *Ancistrocercus inficitus*, and neotropical eusocial wasps, *Polistes instabilis* and *P. versicolor*, show that tettigoniids prey on unguarded wasp nests and may employ chemical or tactile cues to distinguish the nests. Tettigoniids prey on brood in *P. instabilis* nests from which adult wasps are experimentally removed. *Polistes instabilis* and *Polybia occidentalis* wasp workers are not tolerant of tettigoniids roosting near their nests, and tettigoniids near wasp nests behave as if avoiding detection by adult wasps. These observations suggest that predation on brood is an important feature of tettigoniid associations with neotropical wasp nests.

Associations of tettigoniids with active colonies of social wasps in the neotropics have been interpreted as a commensalistic or mutualistic relationship, wherein the tettigoniids gain protection from predators for the duration of their diurnal inactive period and the wasps gain additional warning of predator approach (Downhower and Wilson 1973; Richards 1978). Here I report a case of predation on a wasp colony by the katydid *Phlugis poecila* Hebard (Orthoptera: Tettigoniidae). Combined with observations of interactions of social wasps and green-faced katydids, *Ancistrocercus inficitus* (Walker), roosting near their nests, and with the results of experimental removal of adult *Polistes* wasps from nests with katydids roosting nearby, these observations suggest that an important component of the association is predation on wasp broods by katydids.

Nest predation observations

On 3 August 1990 at 1200h, I discovered a small, newly-founded (preadult emergence) nest of *Polistes versicolor* (Olivier) (Hymenoptera: Vespidae) 2 m above the ground under a *Heliconia* sp. leaf at the edge of a clearing near Gamboa, Republic of Panama. The nest was attended by a single female wasp, presumably the foundress, during observations. A female tettigoniid, *Phlugis poecila*, was resting on the same leaf at a dis-

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tance of 5 cm when the nest was discovered. *Phlugis poecila* is predaceous, though little else is known of its behavior (D. Nickle, pers. comm.).

The *P. poecila* female approached the nest at approximately 5 min intervals over the course of 45 min following nest discovery. On each approach the tettigoniid remained at a distance roughly equal to her antennal length and gently touched both the nest and adult wasp with the distal ends of her antennae; whenever her antennae contacted the wasp the katydid retreated to a distance of between 10 and 30 cm from the nest and remained motionless until the next approach. The wasp made no obvious response to the tettigoniid throughout this period. The wasp departed for 4 minutes on a foraging trip, but the katydid did not approach during this time.

After 50 min of observation I removed the wasp from the nest and placed her in a sealed container. The tettigoniid approached and antennated the unoccupied nest 5 min later, then retreated 3 cm. After 4 min the tettigoniid returned, antennated the nest, then approached and touched the nest petiole and the bases of the cells with her labial and maxillary palpi. The tettigoniid climbed onto the nest and touched the brood cell entrances with her palpi before climbing back to the base of the nest. At this point she held the nest with her forelegs and chewed at the bottom of one brood cell near its attachment to the nest petiole. This chewing continued for 10 min, at the end of which I collected the nest and the tettigoniid.

The damage to the wasp nest was clearly visible at 8X magnification as holes chewed into brood cell bases. A total of three cells bore similar damage, suggesting that the nest had been attacked before my observations. All cells contained larvae, however.

Nest predation experiment

I surveyed 45 active *P. instabilis* de Saussure colonies for the presence of katydids roosting within 1 m of their nests on 8 July 1992 at Palo Verde National Park, Costa Rica. Green-faced katydids were found near 71% of the nests surveyed (X number katydids present = 2.96, sd = 3.45, range = 0 to 17); over 90% of the katydids were roosting within 10 cm of the nests. The number of adult wasps occupying the nests at the time of the survey ranged from 2 to 11 ($\overline{X} = 5.2$, sd = 2.28). None of the wasp nests bore damage, for example holes or tears in brood cell walls, which might suggest attempted katydid predation.

Downhower and Wilson (1973) noted that a green-faced katydid roosting near a *Polistes* sp. nest in Costa Rica fed on wasp pupae after the nest had been moved and the adult wasps had been removed. I removed all adult wasps from five *P. instabilis* colonies on 13 July 1992 between 1930h and 2030h, after nearby katydids had left to forage, to test the hypothesis that brood in unguarded wasp nests would be preyed upon by katydids. I did not otherwise manipulate the nests or katydids. At 600h the following morning 4 to 12 green-faced katydids were present at four of the treated nests. Brood cells in these four nests were apparently chewed open on the sides and their contents partially removed (number of cells damaged ranged from 6 to 15). No katydids were present at the remaining nest, which was undamaged. Four surveys of the manipulated nests were conducted over the ensuing 36 hours. The number of cells damaged increased on the four nests with katydids present, and katydids were observed chewing through cells and consuming brood on each of these nests. The nest without katydids present was not damaged.

Downhower and Wilson (1973) found that *A. inficitus* were able to relocate two *Polistes* sp. nests in the morning after the nests were displaced 1 m from their original site the previous night, and that the nest petioles were especially attractive to the tettigoniids; the adult wasps placed in a nearby cage were not attractive. These results, combined with my observations, suggest that some tettigoniid species are capable of distinguishing wasp nests using chemical or tactile cues, and that the tettigoniids can discriminate between the nest and the adult wasps using these cues. In the case of *P. poecila*, substrate-borne cues were apparently employed in discriminating between the nest and the adult wasp.

Wasp responses to tettigoniids

Ancistrocercus inficitus often perch on twigs within 10 cm of wasp nests, adopting the cryptic posture described for other neotropical orthopterans (Robinson 1969). My observations in Guanacaste, Costa Rica in 1988 and 1991 showed that A. inficitus roosting near eusocial wasp (Polistes instabilis and Polybia occidentalis [Olivier]) colonies were attacked and occasionally driven away after being detected by wasp workers. Though roosting tettigoniids often remained motionless for several hours, initial detection was probably visual, since the wasps often oriented to and approached the tettigoniids following movement. Wasp workers that contacted tettigoniids with their antennae raised their wings, elevated their bodies, and bit the intruders repeatedly (observed on several occasions at one Polistes instabilis nest in 1988 and at two Polybia occidentalis nests in 1991). When attacked by wasps, A. inficitus slowly raised the body part being bitten and only moved away if the wasp worker was especially persistent. A similar response to tettigoniids was noted at a Synoeca sp. colony in Costa Rica (Downhower and Wilson 1973). Social wasps are not tolerant of roosting tettigoniids, though this may be a general response by workers to foreign insects near the nest.

Roosting near wasp colonies may afford protection to predaceous tettigoniids, but it is unclear which potential predators of tettigoniids would be repelled by the wasps (Downhower and Wilson 1973). Both wasp nests and green-faced katydids are fed to nestling trogons (*Trogon* sp.) by their parents in Guanacaste (F. Joyce, pers. comm.).

Association with wasp nests during the daylight hours maximizes the probability that the nest will be unoccupied or occupied by few wasps, since social wasp foragers return to and cluster on their nests at night. This is especially true in relatively young colonies of independentfounding wasps such as *Polistes* spp., however, even a small number of adult wasps present on the nest can apparently deter katydid predation. Further observations of tettigoniids roosting near small wasp colonies are needed to establish the frequency of predation on unmanipulated nests and the impact of tettigoniid predation on wasp colony success.

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